genus Cribraria (in common with the rest of the Heterodermeæ), similar in construction to those of Lindbladia except that they are permanent and not evanescent under the conditions above detailed ; second, the similarity of the sporangia of at least one species, *Cribraria argillacea*, with its practically permanent wall, to those of the stipitate and substipitate forms of Lindbladia effusa var. simplex.

It is, therefore, a legitimate inference, that Lindbladia and Tubulina, although they closely approach each other, having been similarly developed along parallel ordinal and partially parallel generic lines, probably arose from independent and perhaps widely separated points of origin.

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The tendrils of Passiflora caerulea.

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(WITH PLATE XIV.)

I. Morphology and anatomy.

The work recorded in this first paper was undertaken for the purpose of determining the factors in the movements of the tendrils of the Passifloræ, more particularly the movements by which a tendril responds to a stimulus, resumes its original position, or on continuance of the irritation coils permanently, and its subsequent changes while coiled and serving as a support for the weight of the adjacent part of the plant body.

Accepting as entirely tenable the view that the other movements of the tendril are the results of conditions of growth and varying states of turgescence, they will be considered only in so far as they affect the coiling of the organ. With this end in view, attention will be directed to the arrangement of the tissue systems, their relative mechanical value as determined by the structure of the individual cells composing them, the continuity of the protoplasm between cells of similar and dissimilar tissues with reference to the irritability and power of conducting impulse of the parts concerned, and to the physiological changes induced in the motile cells by the stimuli to which this organ responds.

The first investigations on the nature of tendrils of which we have any record are those of Palm[1] and Mohl[2] published within a few weeks ot each other in 1827.

The descriptions in these works are necessarily very meager; the one dealing with the subject from a physiological standpoint while the other reasons from the structural characters alone.

In 1858 Prof. Asa Gray published his paper on the movements of the tendrils of the cucurbitaceous plants [3] which led Darwin to undertake a series of observations which he finally extended to more than one hundred species, the results of which were published in the Journal of the Linnean Society 1865. [4]

Hugo de Vries in his "Zur Mechanik der Bewegung von Schlingplanzen"[5] deals chiefly with the difference of growth of the upper and lower sides of tendrils and the mechanism of movement of twining plants. All of these workers were concerned chiefly with the outward phenomena of movement rather than morphological changes and structural condition. Contemporaneous with these observers and later, much notable work has been done on the organogeny, structure and physiology of tendrils.[6]

To determine the conditions prevailing in the tendril during its period of sensitiveness it was thought necessary to study

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[1]PALM: Ueber das Winden der Ranken. [2]MOHL: Ueber das Winden der Ranken und Schlingpflanzen.

[3]Proc. Amer. Acad. of Science and Arts.

[4]Climbing plants.

[5]Arbeiten des botanischen Institut in Würzburg, 1873, Band I. Heft 3.

[6]BRAVAIS BROTHERS: Annales Sc. Nat. 2 Sér., 1837.—ST. HILAIRE: Leçons de Bot. p. 170. 1841.—DUTROCHET: Comptes rendus. tom. 17. p. 989, Des mouvements revolutifs spontanes, 1843.—SACHS: Lehrbuch der Botanik; Physiology of Plants. —WYDLER: Flora 1853, Pringsheim's Jahrb. 1878, tome 2, page 317.—FRITZ MUELLER: Journal of the Linnean Society, vol. 9.—DE CANDOLLE: Bulletin de la Soc. Bot. de France, 1857.—LEON: *ibid* tom. 5, p. 680, 1858; Gardeners Chronicle 1864, 721, quoted from Darwin.—MCNAB: Trans. Bot. Soc. Edinburgh, vol. 2, page 292.—LOTAR: Essai sur l'anatomie comparée des Cucurbitacèes, Lille, 1871.—SCHWENDENER: Das mechanische Princip im anatomischen Bau der Monocotylen, 1874.—EICHLER: Blüthendiagramme, 2 vol. 1879.—DUTAILLY: Assoc. franc. pour l'Avanc. des Sc., 8 session: Recherches sur les Cucurb. et les Passiflores, 1879.—HABERLANDT: Physiologische Pflanzenanatomie.—VINES: Physiology of plants, 1886; La Sensibilitie et la motilitie.—MORREN: Des Veg. Bruxelles 1885 p. 52.—OTTO MUELLER: Untersuchung über die Ranken der Cucurbitaceen, 1886, in Cohn's Beitræge zur Biol. der Pflanzen.—PENHALLOW: Mechanism of movement of Cucurbita, Vitis, and Robinia. Proc. Roy. Soc. Canada, vol. 4, sec. 4, 1886.—PFEFFER: Zur Kenntniss der Kontaktreize; Untersuchungen aus dem bot. Inst. zu Tübingen, Band I, 1885.—RUSSELL: Recherches sur la Vrille des Passiflores: Bulletin de la Soc. Bot. de France, 189, 1890.—MASTERS: Trans. Linnean Soc., 1878, p. 317.

its development through all stages of growth from the time of its appearance as an axillary papilla till it passed out of the sensitive stage. During the latter periods of growth sections could easily be made with the aid of pith and a common hand clamp and the collodion embedding method,[7] while in the younger stages a modification of the paraffin methods given by Moll, Campbell and Andrews in the BOTANICAL GAZETTE[8] was found to be more satisfactory.

The greatest difficulty, however, was experienced in fixing and hardening the material. The whole organ is in a state of extreme tension and the contact of any reagent on the sensitive concave surface will, unless it has sufficient strength and penetrative power to kill and fix the protoplasmic body instantly, cause the tendril to roll up in a helix, and the form of the wall and contents of the motile cells would be much distorted. A wide range of reagents was tried with but partial success in any case. Alcohol in strengths varying from 1 per cent. to 96 per cent. was found to be useless, as also corrosive sublimate. Potassium nitrate was found to give the best results in a 4 per cent. solution, but caused the organ to form an open helix. Chromic acid distorted the protoplastic structure besides rendering the sections difficult to stain. Schulze's chrom-acetic-osmic solution was useful only in tendrils less than 2 mm. in length. A mixture of one part distilled water and one part saturated solution of bichromate of potassium retained the structures fairly well in many cases, as did also weaker solutions of the same.

By far the best results were obtained by the use of acetic alcohol of the following composition: 1 part glacial acetic acid; 6 parts absolute (or 96 per cent.) alcohol; 3 parts chloroform.[9] The tendril must be carefully cut from the stem with the least possible jarring and avoiding all contact with the sensitive lower surface, and then placed in the fixative which must be in a vessel of sufficient dimensions to receive its entire length in a horizontal position. The action of the fluid will cause it at first to curve slightly, and then to regain its former position. After two or three oscillations of this sort it will regain and keep nearly its original form. After remaining in this fluid for a time varying from 20 to 30 minutes, it was re-

7. Proc. Am. Soc. of Microscopists, 1890. THOMAS: Botanical Gazette, Nov. 1890.

8. January and June, 1888; July, 1890.

9. LEE: Microtomists Vademecum, 1890.

moved, cut into convenient lengths and placed in 96 per cent. alcohol which was changed several times to remove the acid.

Sections were made with a Cambridge rocking microtome, fastened to the slide in series and after the removal of the paraffin stained in a hæmatoxylin-eosin mixture of the following composition: distilled water, 5 parts; hæmatoxylin (Delafield's) 3 parts; eosin (watery solution) 2 parts. The sections were allowed to remain in the staining fluid 20 minutes. After dehydrating and clearing they were mounted in Canada balsam dissolved in oil of cajeput. The differentiation afforded by this stain can hardly be excelled. The nuclear structures take a dark purple color while the remainder of the cell contents and the walls take on various shades of red according to density.

The tendrils of Passiflora cærulea are filamentous organs springing from the axils of the leaves, often reaching a length of 30 cm., tapering from a diameter of 2 mm. at the base to 1 mm. at the tip before coiling. When 1–3 cm. in length the whole surface often has a reddish purple tinge due to color bodies in the subepidermal cells. With growth the color becomes less vivid and is distributed over the surface in ill defined longitudinal bands. It often disappears entirely from the lower surface, being hidden by the deeper tinge of the chlorophyll.

The tendril makes its appearance as a cone of meristem tissue on the side of the growing point in the axil of a leaf. Shortly after its appearance while it is yet less than .5 mm. in length, there is formed on its summit an irregular cup-shaped depression (fig. 4) by reason of the excessive growth in length of the periblem, that of the upper side being greater. The continuance of this unequal growth causes the cup in the full-grown tendril to become lateral (fig. 5). About the time the cup has assumed the form in fig. 4, spiral vessels make their appearance just below it, followed by companion and sieve cells. The point of most rapid growth passes backward with the elongation of these fibrovascular elements until at the time of coiling it is found at a short distance below the middle of the organ.

When the tendril has reached this stage three distinct regions may be distinguished: the base or non coiling part, 3–4 cm. in length; the middle region or coiling portion comprising the greater part of the organ, which is generally slightly curved; and the sharply curved or hooked tip, 4–6 mm. in length. These three regions show some well marked differences in structure and outline. The whole organ shows a bilateral organization which is least apparent in the base and most pronounced in the portion having the greatest power of movement, a recognized correlation given by Dr. Otto Müller.[10]

The basal portion is broadly oval in outline with just a trace of flattening on the lower side ; the middle portion is oval with its lateral much greater than the transverse diameter, while the lower surface is distinctly flattened. The tip is nearly circular in outline, and bears at its extreme end the cup-shaped formation above mentioned. Along the convex upper and lateral sides of the tendril are several obscure angles which are mostly absent from the lower concave surface.

The internal structure of these parts shows corresponding differences. The arrangement in the middle portion is as follows: The epidermis consists of a layer of rectangular cells with the longest diameter parallel to the long axis of the tendril (figs. 1, 2, 3, *a*). Occasional stomata are found distributed equally over both surfaces.[11]

Beneath the epidermis is a layer of collenchyma with thickenings so disposed that that the tangential are much heavier than the radial walls (figs. 1, 2, 3, *b*). Scattered through this tissue are the color bodies mentioned above. At the obtuse angles of the tendril this layer is three cells in thickness, at other places it decreases to one.

Internal to this is a layer of loosely arranged thin walled parenchyma of varying size, containing in the outer rows of cells an abundance of chlorophyll and protoplasm (figs. 1, 2, 3, *c*). The inner rows of cells bordering on the bast are richly loaded with starch, constituting the starch layer of Sachs.[12]

Through the entire layer are occasional crystals of calcium oxalate. The cells of this layer on the convex side are uniformly larger than those on the concave side, leading to a corresponding difference in thickness of the layer. The in-

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[10] "Soweit also die Ranke central gebaut ist, zeigt sie kein Krummungsvermögen: soweit sie bilateral gebaut ist, soweit betheiligt sie an den Einkrummungen." l. c., p. 120.

[11] PFEFFER: Zur Kenntnis der Kontaktreize, Par. 9.

[12] Physiology of Plants, p. 358 ; STRASBURGER : Das botanische Practicum, p. 132.

tercellular spaces are large and plentiful by reason of the peculiar manner of junction of conical ended cells. In many cases, however, the entire ends of adjacent cells are pressed closely together, presenting the phenomenon (seen in figs. 2 and 3, *c.*) of one cell sending a protrusion into the cavity of another. It is evident that these cells by both structure and arrangement are well fitted to undergo great variations in size, while the large intercellular spaces, affording plentiful space for the reception of expelled cell sap, make possible rapid changes in the tension of this tissue. The parenchyma is connected with the central pith by medullary rays, two to four cells in height, in the region of secondary growth.

Immediately internal to the starch sheath is the bast region consisting of thin walled, closely packed cells, containing a large amount of dense protoplasm. These are in a condition of rapid growth which gradually becomes less active as the tendril approaches maturity, when they take on excessive wall thickenings, in a manner very similar to that of Cucurbita (fig. 1, *d.*).[13] When the tendril has only reached a fraction of its length this tissue has formed a continuous band interrupted only by the medullary rays.

About the time of maturity the cambium makes its appearance and soon forms a ring of secondary growth on the inner side of the bast, and retains its activity even after the coiling. The primary xylem elements (fig. 1, *e*) are about ten in number; half are disposed in a nearly straight row across the concave side, while the remainder are in an approximate semicircle to conform to the outline of the convex side. Each bundle consists of two or three spiral vessels arranged radially (with generally an annular vessel placed axially), which show marked lignification even in the immature organ. The formation of secondary bundles takes place in such manner on the concave side that a continuous band of wood is formed here, while the xylem elements of the other side retain their individual character until after coiling. The central pith is composed of large parenchyma cells containing some protoplasm.

The basal portion differs from this in its regular oval outline, symmetrical arrangement of the xylem, heavier thickening of the collenchyma, and early formation of a continuous distinct cambium zone. Lignification has extended slightly

[13] PENHALLOW: Proc. Roy. Soc. Canada, vol. 4, sec. 4, 1886, p. 54.

to the pith, and parenchyma in the xylem, which has three or four spiral vessels besides an annular vessel in each bundle. The central pith is generally found torn apart forming the lysigenetic intercellular spaces of De Bary.[14]

The structure of the tip, however, is widely different from that of either of the regions just described. Near the extremity of the concave side may be seen the oval aperture of the cup formation lying transversely to the length of the tendril, appearing white because of the absence of chlorophyll in the tissues beneath. The cavity is .3–.4 mm. across in a direction parallel to the long axis of the tendril and about .8 mm. in a transverse measurement, with a depth of .5 mm. (fig. 6, *e*). The epidermal cells of this region become smaller toward the extremity and are smallest on the floor of the cavity (fig. 6, *a*, *a'*). The collenchyma is composed of one row of shortened, strongly thickened cells terminating at the rim of the cup (fig. 6, *b*, *b'*).

The chlorophyll layer undergoes no changes on the concave side except a slight reduction in size and an increased density of the protoplasm, a feature common to the region except certain cells near the cup. The parenchyma layer of the convex side is relatively very thick, and is composed of very angular, much distorted cells, many of which have their long diameters perpendicular to the surface as seen in fig. 6, *c*.

The bast and cambium decrease in size and disappear entirely shortly after they enter this region. The scattered bundles of xylem of the convex side and the band of the concave side converge as they near the cup and are separated only by a thin spindle of pith. The termination of the tracheary tissue is marked by a mass of epithema,[15] composed of long, slender cells with oblique ends, appearing as a continuation the tracheæ, and touching directly the epidermal layer of the cup without the intervention of the collenchyma layer.

All the tissues of the tendril are abundantly supplied with pits, especially the parenchyma of the pith and cortex, which have numerous simple pits, oval in form, arranged transversely, with the torus present. The inner side and radial walls of the parenchyma of both the concave and convex surfaces communicate with the adjacent cells by similar structures; those of

[14] Comparative Anatomy of Phanerogams and Ferns, Eng. Ed., p. 200.

[15] De Bary: Comp. Anat. of Phanerogams and Ferns, Eng. Ed., pages 375–376.

the collenchyma being most numerous on the tangential walls. The markings of fibrovascular elements are of the common form in this type of plants. The arrangement of the protoplasmic body of the organ with reference to density and composition, bears a direct relation to the sensitiveness of any part of the organ. The protoplasm is most dense and richly granular in the epidermis and chlorophyllous cells of the concave surface near the tip. The density decreases as it passes back into the middle region where it is quite uniform throughout. The contents of the epidermal cells and collenchyma of this side take the stain most deeply as does the epidermis of the convex side, which, as well as the underlying tissue, is very similar over the entire surface.

It may be assumed in conclusion, that the concentration of the protoplasm in the epidermal layer has a direct connection with irritability, that the movements of the organs are due to changes in the chlorophyll layer and that the disposition of the xylem elements is favorable to rapid flexion and extension, and that the abundant supply of reserve food material is a provision for the rapid growth and fixation of the tendril upon coiling.

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Explanation of Plate XIV.—Fig. 1. Half cross section of middle portion of tendril.—Fig. 2. Longitudinal section of convex side of same.—Fig. 3. Longitudinal section of concave side of same. *a*, *a'*, epidermis; *b*, *b'*, collenchyma; *c*, *c'*, chlorophyll parenchyma; *d*, bast; *e*, xylem; *f*, pith.—Fig. 4. Longitudinal section of tip of tendril showing cavity, *a*.—Fig. 5. Cavity of same seen from end.—Fig. 6. Longitudinal section through tip of mature tendril. *a*—*d*, same as in fig. 1; *e*, cavity; *f*, epithema.—Fig. 7. Diagram showing distribution of protoplasm in tip and part of middle region of tendril.

An apparatus for determining the periodicity of root pressure.

M. B. THOMAS.

(WITH PLATE XV.)

The study of the periodicity of root pressure has received much attention from physiol o gical botanists and the results of quite extended researches \\ave been published by Sachs, Hofmeister, Detmer and others. The work has been done with very crude apparatus consisting simply of a manometer